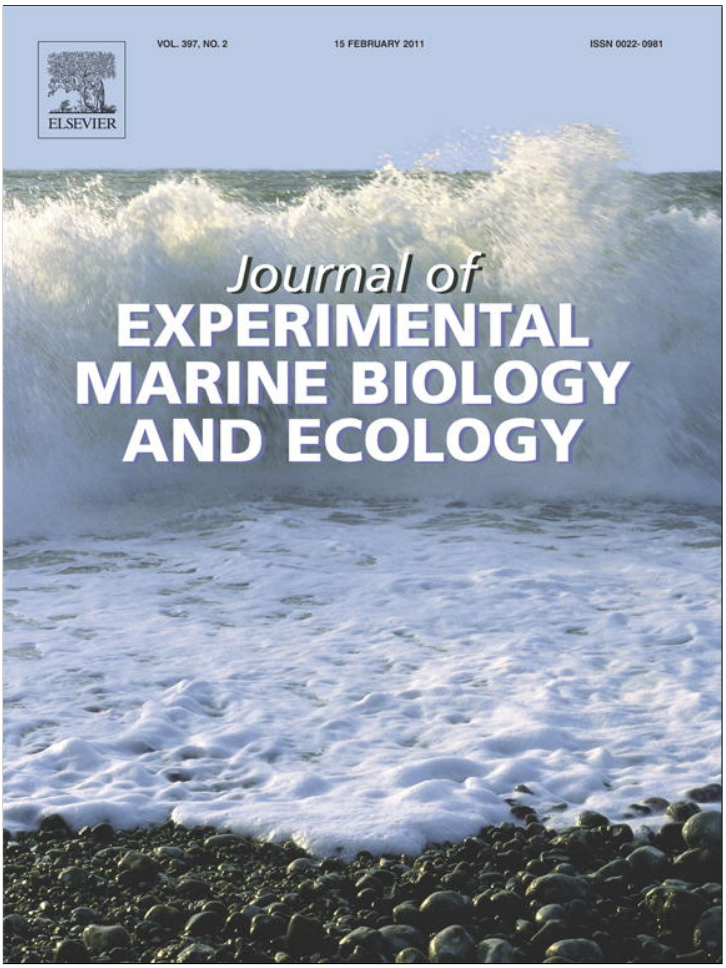

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Variation in penaeid shrimp growth rates along an estuarine salinity gradient: Implications for managing river diversions

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ABSTRACT

Freshwater inflows from river diversions may affect nekton populations by altering the salinity and temperature of estuarine waters. To investigate the influence of these environmental variables on the growth and survival rates of brown shrimp *Farfantepenaeus aztecus* and white shrimp *Litopenaeus setiferus*, we conducted field experiments in May and September 2007 to expose experimental animals to the range of different combinations of salinity and water temperature that commonly occur in an estuarine environment. Growth rates for shrimp held in mesocosms for approximately 7 days were compared among four locations and three treatments; locations were identified by the dominant marsh vegetation and distance from the Gulf of Mexico (low to high salinity: Intermediate, Brackish, Saline UE = Saline Up Estuary, Saline DE = Saline Down Estuary). At each location, the treatments were replicated four times and included shallow water with additional food, shallow water without food added, and deeper water (an attempt to expose animals to lower temperatures). Our experiments were designed to test the null hypothesis that shrimp growth and survival rates did not differ by location or treatment. Both brown shrimp and white shrimp grew more slowly at the Intermediate than higher salinity locations. Potential prey (benthic infauna) biomass was relatively low at both the Intermediate and Brackish locations in May, and both shrimp species consistently grew faster in mesocosms where food was added. We conclude that reduced growth in low salinity environments is likely due to the combined effects of increased metabolic costs and less food in these areas. River diversions that reduce estuarine salinities over a large portion of available habitat during peak recruitment periods may reduce overall growth rates and shrimp productivity in the affected areas.

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1. Introduction

Most major river systems have been greatly modified for navigation, settlement, and commerce (Day et al., 1997; Cattrijse et al., 2002). Flood control projects intended to protect human development within river floodplains often decoupled rivers from adjacent estuaries. The Mississippi River, for example, is confined within a complex system of levees and no longer allowed to flow freely into the estuaries of southeastern Louisiana (Boesch et al., 1994). An unintended consequence, a cutoff of the sediment supply to adjacent estuaries, has been identified as one of the causes for the high loss rate of coastal wetlands in the Mississippi River deltaic plain (Day et al., 2000), where most landloss from coastal Louisiana has occurred (Britsch and Dunbar, 1993). Wetland loss rates along the Louisiana coast have ranged from 66 to 108 km^2 $year^{-1}$ since 1958 (Britsch and Dunbar, 1993).

In response to this landloss problem, several large capacity water-control structures are being planned that would reconnect the Mississippi River to the estuaries of southeastern Louisiana to restore coastal wetlands. Existing structures (e.g., Caernarvon and Davis Pond) already divert some freshwater from the Mississippi River into nearby estuaries, but the capacity of these structures is relatively small (<350 m^3 s^{-1}). River diversions increase the inflow of freshwater to estuaries, and in doing so influence numerous estuarine characteristics that affect primary and secondary productivity (Alber, 2002). These freshwater inflows directly alter the salinity, water temperature, and other environmental variables of estuarine waters, which can influence the movement and distribution of estuarine animals (Szedlmayer and Able, 1993; Thiel et al., 1995; Baltz and Jones, 2003; Harrison and Whitfield, 2006; Piazza and La Peyre, 2007; Childs et al., 2008).

Changes in the estuarine environment also can affect the survival, growth, and productivity of estuarine animals, some of which support important coastal fisheries. For example, brown shrimp *Farfantepenaeus aztecus* production in coastal Louisiana has been related to the salinity and temperature of estuarine nursery areas (Barrett and Gillespie, 1973). The young of both brown shrimp and white shrimp

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Litopenaeus setiferus use estuarine nursery areas, and these species support a valuable penaeid shrimp fishery in the Gulf of Mexico (Zimmerman et al., 2000).

Data from the scientific literature that would inform management decisions for operating diversion structures to minimize impacts to the shrimp fishery are inadequate. Only a few laboratory studies have examined the effect of water salinity and water temperature on growth and survival of brown shrimp and white shrimp. Penaeid (both brown shrimp and white shrimp) postlarvae survived and grew equally well in salinities of 2–40 in a laboratory study where water temperatures were held between 24.5 and 26.0 °C (Zein-Eldin, 1963). When temperatures were <15 °C, however, the survival of brown shrimp postlarvae decreased in salinities <5 (Zein-Eldin and Aldrich, 1965), and brown shrimp were more tolerant than white shrimp of temperatures ≤15 °C (Zein-Eldin and Griffith, 1969). Relatively little work has been conducted on the effects of temperature and salinity on larger juvenile penaeids. In laboratory experiments on juveniles, Saoud and Davis (2003) reported growth of brown shrimp to be significantly higher at salinities of 8 and 12 than 2 and 4, but water temperature was not varied and white shrimp were not examined. Survival and growth rates of juvenile penaeid shrimps have not been documented for the range of different combinations of water temperature, salinity and shrimp size that commonly occur in an estuarine environment. In addition, the effects of these variables have not been examined experimentally in the field, and results of laboratory experiments do not always reflect impacts in natural environments (Hairston, 1989; Morin, 1998).

The uncertainty surrounding the environmental requirements of brown shrimp and white shrimp is surprising given the importance of the fishery for these species. A better understanding of the relationships between water temperature and salinity and growth and survival is needed to adaptively manage large water diversion structures. The objective of our study was to examine the relationships between shrimp growth and long-term salinity patterns using short-term field experiments. We also attempted to measure the effect of temperature by including a depth variable in the experimental design. We measured growth of juvenile brown shrimp and white shrimp in mesocosms placed at different water depths along an estuarine salinity gradient in the Barataria Bay system of Louisiana.

2. Methods

We selected four locations along a salinity gradient within the Barataria Bay estuary of southeast Louisiana for each of our two experiments (Fig. 1). The long-term salinity gradient is revealed by vegetation-salinity zones defined and mapped by Chabreck (1972) and Linscombe and Chabreck (2001). We established locations within the Intermediate, Brackish, and Saline zones to expose experimental animals to a wide range of historical salinity conditions, while also expecting ambient salinities to vary in relation to these locations. These zones are comparable to the Oligohaline, Mesohaline, and Polyhaline zones, respectively, of the Venice System (Anonymous, 1958; Visser et al., 1998). We changed the experimental location within the Intermediate zone after the brown shrimp experiment to reduce wave exposure to the mesocosms. Two locations were established within the Saline zone for each experiment. The Saline DE (down estuary) location was 13.7 km nearer the Gulf of Mexico than the Saline UE (up estuary) location. Tides in the study area are predominantly diurnal and have a mean daily range of 0.3 m (Orlando et al., 1993). The experiments were conducted in 2007 when each species was locally abundant in our study area. Brown shrimp growth was measured in May and white shrimp in September.

Mesocosms were deployed at each location 2 days before initiating an experiment. Each mesocosm was a 1.07 m-diameter, 0.76 m tall, bottomless cylinder that enclosed 0.89 m^2 of habitat (shallow non-vegetated bottom) and was constructed of 3.2 mm mesh nylon netting, 2 fiberglass rings, and plastic pipe. The top of the mesocosm also was covered with 3.2 mm netting, but material could be passed through a small closable (11.4 cm diameter, 15 cm long) sleeve sewn into the top. Each enclosure was set in place over shallow non-vegetated bottom by pushing it through the water to the bottom substrate, and no effort was made beforehand to remove potential competitors or predators from the mesocosm site. The bottom edge of the mesocosm was pushed 10–15 cm into the substrate to prevent escape by experimental animals or entry by predators. Metal rods were inserted into the three plastic pipes supporting the walls of each mesocosm and driven into the substrate to hold the mesocosm in place. We then collected and pooled three (2.5 cm deep × 5.0 cm diameter) benthic cores from undisturbed sediment around the outside perimeter of each mesocosm. These core samples were used to measure potential prey (benthic infauna) availability at each mesocosm site. Core samples were washed through a 0.5 mm mesh sieve, and the material retained preserved in formalin, labeled, and returned to the laboratory for processing.

The experimental design incorporated three treatments (with four replicate mesocosms per treatment) within the four locations. At each location, eight mesocosms were placed in shallow water along the shoreline (mean distance from marsh = 2.5 m in May and 2.0 m in September). Half of these shallow-water mesocosms were randomly assigned to receive additional food (0.78 g Rangen Shrimp Production Formula 35™ enclosure^{-1} day^{-1}) during an experiment (SF = Shallow Food treatment), whereas no food was added to the other four mesocosms (SNF = Shallow No Food treatment). Rangen 35 is commercially available and has been shown to sustain growth and survival of penaeid shrimp (Davis and Arnold, 1994). Four additional mesocosms at each location were placed farther from shore (mean distance from marsh = 18 m in May and 25 m in September) and in deeper water to potentially expose the enclosed experimental animals to lower temperatures (D = Deep treatment). Mesocosms in each group were spaced at least 8 m apart.

On the day an experiment was to be initiated, we collected shrimp in the study area using small bag seines and immediately transferred them to aerated containers. Experimental shrimp were collected from two locations (Brackish and Saline DE) because shrimp populations were too low at the Intermediate location (Rozas and Minello 2010) to stock the mesocosms with shrimp from this location within the time allotted for setting up each experiment. Moreover, collecting animals from a single location would have required additional handling of shrimp and a lengthy period for acclimation before initiating each experiment. The experimental shrimp used at the Intermediate and Brackish locations were collected at the Brackish location, and those used at the Saline UE and Saline DE locations were collected at the Saline DE location. Experiments could not be initiated at all four locations on the same day because of time constraints. Therefore, we initiated experiments at the Saline locations on one day, and the Intermediate and Brackish locations the next day. When enough animals for an experiment had been collected, individuals were tagged, measured to the nearest mm in total length (TL), and then assigned randomly to a mesocosm. We used five individuals per mesocosm in each experiment. This stocking density (5.6 shrimp m^{-2}) allows us to compare our results with previous work using a similar density (Rozas and Minello, 2009; Baker and Minello, 2010) and, for most locations, it is within the upper range of naturally occurring densities (individuals m^{-2}) measured at high tide for shrimp in marsh ponds of Barataria Bay (Rozas and Minello, 2010). These densities are likely lower than those expected at low tide when shrimp are concentrated within subtidal areas. We used a relatively large size range of experimental shrimp to broaden the inference of our results, but we also wanted to ensure that any relationship between initial size and growth would not confound our results (Rozas and Minello, 2009). Therefore, we separated shrimp into five size categories prior to tagging, and one individual from each size class was placed into each mesocosm. We used Visible Implant Elastomer (VIE™) tags injected into the

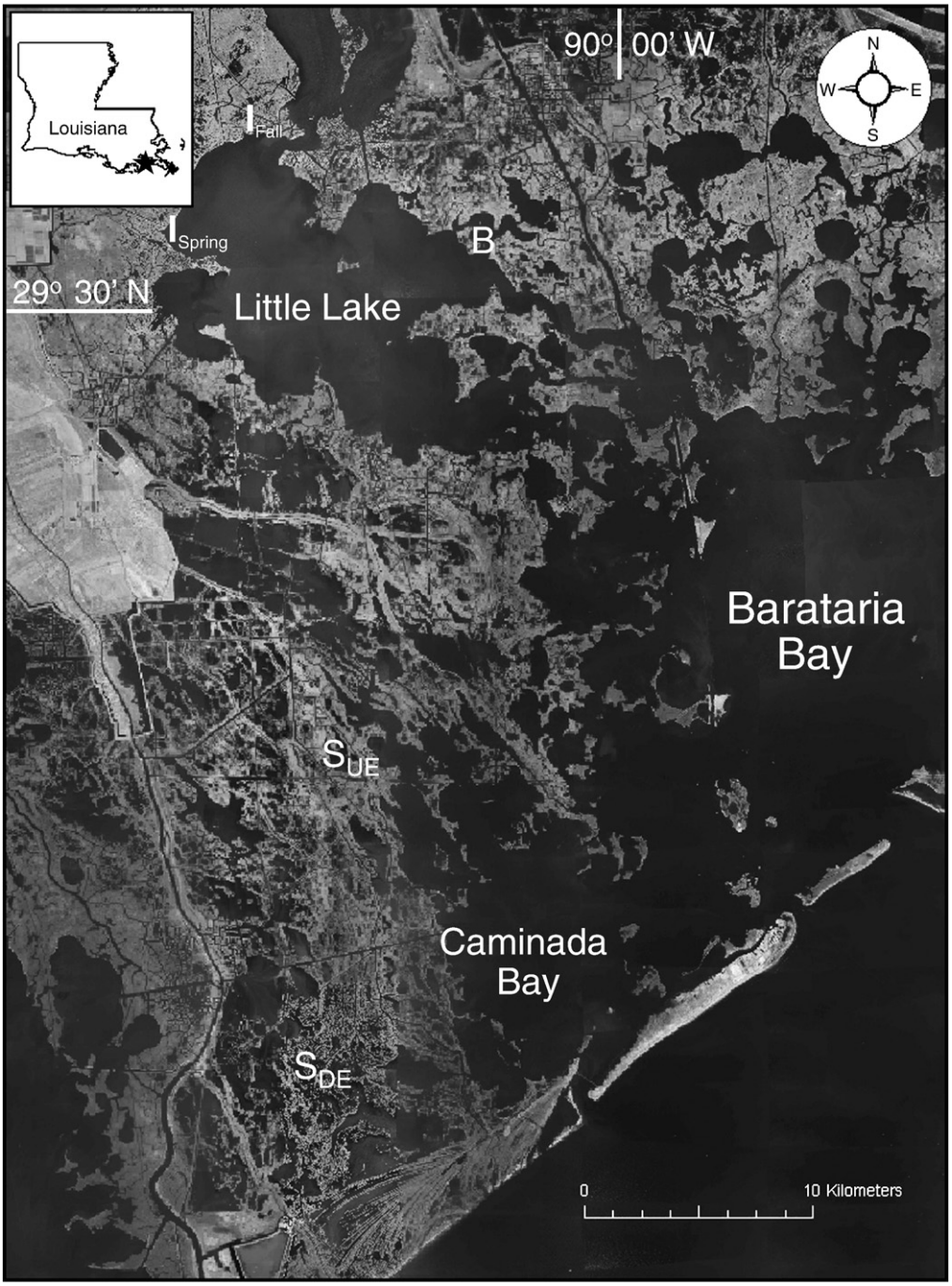

Fig. 1. Map of the study area within the Barataria Bay estuary of southeastern Louisiana. Experimental mesocosms were located along the estuarine salinity gradient within the Intermediate, Brackish, and Saline zones. The mesocosm locations are labeled as follows: I_{Spring} = Intermediate for brown shrimp experiment, I_{Fall} = Intermediate for white shrimp experiment, B = Brackish, S_{UE} = Saline Up Estuary, and S_{DE} = Saline Down Estuary.

abdominal muscle tissue to individually mark (i.e., unique mark for each size class) all experimental shrimp. Our unpublished laboratory experiments indicate that these tags do not affect shrimp growth or survival, and no effect on growth was observed using these tags on juvenile blue crabs (Davis et al., 2004).

We measured the total length (TL) of shrimp at the beginning and end of an experiment along with the final wet weight. We estimated initial weights of experimental shrimp using length–weight relationships derived from other shrimp collected at the beginning of each experiment; this approach was used to reduce handling effects on experimental animals. We derived these length–weight relationships (equations) after first log transforming the size and weight data to ensure a linear relationship and then regressing Log_{10} weight by Log_{10} TL.

We measured environmental variables that might affect growth both within and outside of mesocosms to determine whether experimental artifacts affected our results. Selected mesocosms were instrumented with Onset™ recorders (for water temperature) and Hydrolab™ Datasonde 3 multiparameter water quality loggers (for water temperature, salinity, DO = dissolved oxygen concentration) to continuously measure environmental conditions during the experiments. Water depth, water temperature, and DO also were measured at each mesocosm during the day 6–7 times during each experiment. The water depth measured at each mesocosm during daily monitoring was used with continuously recorded water level data from a NOAA tide gauge and a temporary tide gauge to calculate flooding durations for mesocosms at each location. The daily

monitoring data also were used to check the accuracy and assess the reliability of the instruments used to continuously monitor selected mesocosms.

Each growth experiment was run for approximately 7 days. At the end of an experiment, we collected the shrimp using dip nets after carefully lowering a drop sampler (1.14 m diameter fiberglass cylinder) over the mesocosm, partially disassembling the mesocosm and lifting it out of the drop sampler. The water inside the drop sampler was then removed with a trash pump, and any animals missed with the dip nets were collected by hand. The method was similar to that used by Zimmerman et al. (1984) to clear a drop sampler. We immediately placed the animals recovered from the mesocosms on ice and weighed and measured each tagged animal within 12 h to determine their final size. Because TL could not be measured for shrimp with broken rostrums, we estimated the TL of these shrimp based on their final weight from length–weight equations derived as described above for initial lengths. We determined growth rates for each recovered experimental animal by subtracting the initial size measurement (TL or wet weight) from the final size measurement and dividing this difference by the duration (in days) of the experiment.

Unmarked fishes and decapod crustaceans were recovered when we removed the experimental shrimp from the mesocosms. Some of these animals likely were trapped inside the mesocosms when the mesocosms were deployed before initiating each experiment. These trapped organisms could have affected the growth or survival of experimental shrimps through competition or predation. All animals recovered from each mesocosm were identified to the lowest feasible taxon. We measured the size of each unmarked animal and pooled individuals of each species in a sample to determine biomass (wet weight).

3. Data analyses

We considered the mean growth rate (mm d^{-1} or mg d^{-1}) from multiple individuals of shrimp recovered from each mesocosm as a single observation in our analyses. We used a 2-way ANOVA to test the null hypothesis that growth rates of experimental animals were similar among the four locations (Intermediate, Brackish, Saline UE and Saline DE) and three treatments (D, SNF, SF). We also used this ANOVA to test for a significant interaction between location and treatment. When the main effect of location was significant at the 0.05 level, we used Games–Howell post-hoc tests to compare growth rates among the four locations (Day and Quinn, 1989). These results allowed us to compare growth of experimental animals between all possible location pairs. If the main effect of treatment was significant, we used *a priori* contrasts to test for differences in growth between shallow and deep sites where shrimp had presumably been exposed to different water temperatures (SNF vs. D) and to determine whether the addition of food had increased growth rates (SNF vs. SF). We used this same analysis to compare the biomass of potential benthic prey among locations and treatments and to test for differences among treatments in the number of penaeid shrimp recovered from each mesocosm experiment.

We used the slope heterogeneity test to determine whether data from the two source locations could be combined before computing a length–weight relationship for estimating initial weights of the shrimp for each experiment (Quinn and Keough, 2002; Hansen et al., 2007). ANCOVA was used to compare slopes of the regression lines describing the length–weight relationships for shrimp collected from the two source locations. If the length–weight interaction in the analysis was not significant, the slopes were assumed to be equal, and the data from the two source locations were combined before computing an overall length–weight relationship (Hansen et al., 2007).

We examined scatter plots and used regression analysis to explore potential relationships between shrimp growth rates and competitors/predators. We compared growth rates in biomass with penaeid biomass, crustacean biomass, and total biomass measured from both marked and unmarked animals recovered from the experimental mesocosms. We also compared the number of recovered marked shrimp (survivors) with predator biomass to test for a possible relationship between the survival of experimental animals and predation risk. In addition, we used regression analysis to look for possible size-related differences in shrimp growth rates and to examine the potential relationship between shrimp growth rates and the biomass of potential benthic prey. We considered alpha levels of 0.05 to be significant in all results. We conducted statistical analyses using SuperANOVA (Version 5 Ed., Abacus Concepts, Inc., Berkeley, CA, 1989), Microsoft Excel (Version 11.3.7, Microsoft Corporation, Redmond, WA, 2004) and SAS (Version 9.1, Cary, NC, 2002).

4. Results

Tides were relatively high during both experiments, and mesocosms remained constantly flooded. An analysis of tide gauge data showed that even in the shallowest mesocosm, the water depth never fell below 20 cm and 29 cm during the May and September experiments, respectively.

Water temperature was measured continuously during each experiment at 18–19 selected mesocosms (Table 1). Continuously recorded water temperature data from the Onset™ recorders were considered reliable, as these data appeared to match the data we collected through daily monitoring. Based on these continuous data, mean (and SE) water temperatures at the four locations were: May: Intermediate = 27.6 ± 0.05 °C, Brackish = 27.3 ± 0.06 °C, Saline UE = 27.0 ± 0.05 °C, Saline DE = 26.9 ± 0.07 °C and September: Intermediate = 27.7 ± 0.03 °C, Brackish = 27.7 ± 0.04 °C, Saline UE = 28.1 ± 0.04 °C, and Saline DE = 27.9 ± 0.05 °C. No significant difference was detected in mean water temperature between shallow and deep treatments in either experiment (May: shallow = 27.3 °C vs. deep = 27.2 °C, ANOVA: MS = 0.644, F = 0.264, p = 0.607; September: shallow = 27.9 °C vs. deep = 27.8 °C ANOVA: MS = 0.246, F = 0.225, p = 0.635). Water temperatures fluctuated over the diel cycle, but were concordant among locations, and when we continuously monitored water temperatures inside and outside the same mesocosm, the temperatures inside the mesocosm tracked the outside temperature.

Salinity and DO data were collected continuously during the experiments at 8–14 and 4–8 selected mesocosms, respectively (Table 1). Based on reliable data from continuous measurements, mean salinities (±SE) in May were: Intermediate = 2.1 ± 0.04, Brackish = 5.2 ± 0.13, Saline UE = 17.3 ± 0.04, Saline DE = 20.6 ± 0.05 and in September were: Intermediate = 1.4 ± 0.02, Brackish = 5.3 ± 0.08, Saline UE = 13.6 ± 0.04, Saline DE = 24.7 ± 0.12. Salinity gradually decreased during the May experiment at all but the Saline DE location, whereas salinity was relatively constant during the September experiment (Fig. 2). Salinity measured inside the experimental mesocosms tracked the salinity measured on the outside during these experiments.

The range in DO from continuous measurements taken outside the mesocosms was 1.9–9.8 mg L^{-1} (mean = 5.6 ± 0.04 mg L^{-1}) in the May experiment and 1.8–9.1 mg L^{-1} (mean = 5.5 ± 0.04 mg L^{-1}) in the September experiment. Mean (±SE) DO concentrations at the four locations based on reliable data from continuous measurements were: May: Intermediate = 6.5 ± 0.06, Brackish = 5.7 ± 0.07, Saline UE = 5.2 ± 0.09, Saline DE = 5.4 ± 0.06 and September: Intermediate = 6.1 ± 0.04, Brackish = 6.5 ± 0.06, Saline UE = 5.2 ± 0.07, Saline DE = 3.9 ± 0.07. Diel fluctuations were large, with lows in the early morning and highs during the afternoon (Fig. 3). These fluctuations inside the mesocosms tracked those outside, although DO concentrations were approximately 0.5 mg L^{-1} lower inside than outside.

Table 1
Methods used to collect environmental data during the growth experiments conducted with brown shrimp and white shrimp at four locations and on four dates. The variables measured by each method, sampling frequency, and the number of monitored experimental enclosures also are given. Monitored enclosures are included in the count only if the recorded data were found to be reliable. WTemp = water temperature, DO = dissolved oxygen, Sal = salinity, WDepth = water depth, * = enclosures monitored with 2 (1 inside and 1 outside) meters.

Species	Dates	Location	Method	Variables measured	Sampling frequency	Enclosures monitored
Brown shrimp	May 7–14, 2007	Saline UE	Daily monitoring	WTemp, DO, Sal and WDepth	Once d^{-1} for 7 days	All
			Temperature loggers	WTemp	Hourly	3D, SF and SN
			DataSondes	WTemp, DO and Sal	Hourly	2D and 2SF
Brown shrimp	May 7–14, 2007	Saline DE	Daily monitoring	WTemp, DO, Sal and WDepth	Once d^{-1} for 7 days	all
			Temperature loggers	WTemp	Hourly	2D, SF and SN
			DataSondes	WTemp, DO and Sal	Hourly	D, D* cage only, SN, SN*cage only
Brown shrimp	May 8–15, 2007	Intermediate	Daily monitoring	WTemp, DO, Sal and WDepth	Once d^{-1} for 6 days	All
			Temperature loggers	WTemp	Hourly	2D, 2SF and SN
			DataSondes	WTemp, DO and Sal	Hourly	2D and 2SN
Brown shrimp	May 8–15, 2007	Brackish	Daily monitoring	WTemp, DO, Sal and WDepth	Once d^{-1} for 6 days	All
			Temperature loggers	WTemp	Hourly	2D, 2SN and SF
			DataSondes	WTemp, DO and Sal	Hourly	SF and SN
White shrimp	September 13–20, 2007	Saline UE	Daily monitoring	WTemp, DO, Sal and WDepth	Once d^{-1} for 6 days	All
			Temperature loggers	WTemp	Hourly	2D, SF and SN
			DataSondes	WTemp, DO and Sal	Hourly	D and SN
White shrimp	September 13–20, 2007	Saline DE	Daily monitoring	WTemp, DO, Sal and WDepth	Once d^{-1} for 6 days	All
			Temperature loggers	WTemp	Hourly	2D, 2SF and SN
			DataSondes	WTemp, DO and Sal	Hourly	D and SN
White shrimp	September 14–21, 2007	Intermediate	Daily monitoring	WTemp, DO, Sal and WDepth	Once d^{-1} for 6 days	All
			Temperature loggers	WTemp	Hourly	2D, D cage only, SF and SN
			DataSondes	WTemp, DO, Sal	Hourly	D* cage only and SN* cage only
White shrimp	September 14–21, 2007	Brackish	Daily monitoring	WTemp, DO, Sal and WDepth	Once d^{-1} for 6 days	All
			Temperature loggers	WTemp	Hourly	2D, SF and SN
			DataSondes	WTemp, DO and Sal	Hourly	SN

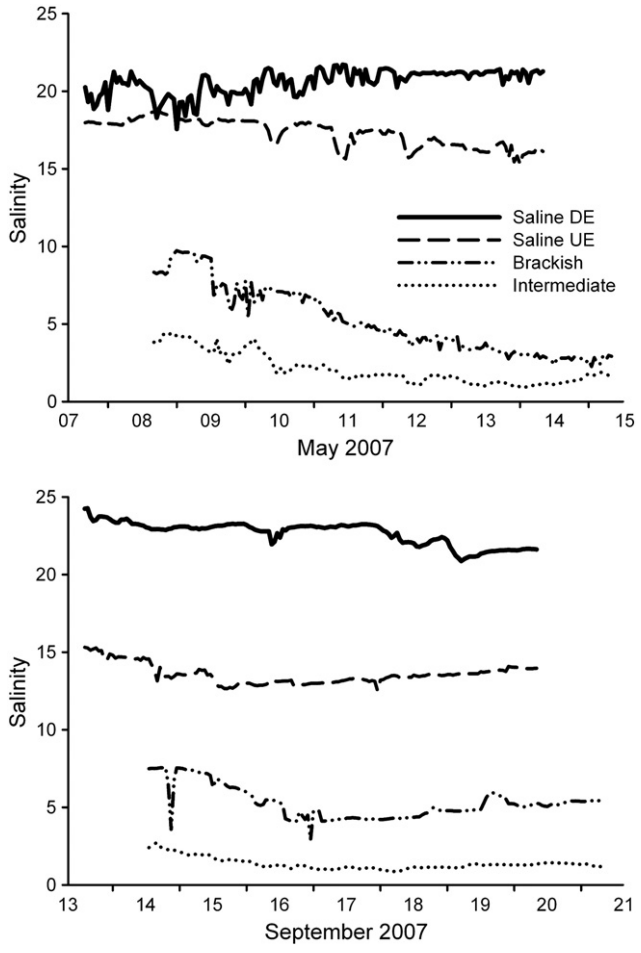

Fig. 2. Plot of salinity measured hourly during the May and September 2007 experiments from one recorder at each location: Intermediate, Brackish, Saline UE = Saline Up Estuary, and Saline DE = Saline Down Estuary.

The brown shrimp and white shrimp used in the experiments ranged in size from 32 to 72 mm TL, but most were small individuals (Table 2). These juvenile shrimp reflected the size of animals most abundant in the study area when the experiments were conducted.

Our analysis detected no significant length–weight interactions in the slope heterogeneity test comparing data from the two source locations in each experiment (ANCOVA, May: $p = 0.4243$, September: $p = 0.0790$). Therefore, we combined the data from the two source locations (Brackish and Saline DE) in each experiment prior to deriving length–weight relationships (equations) for estimating initial weights of experimental animals.

Growth rates appeared weakly related to initial size, but only for white shrimp. Brown shrimp growth rates were not related to the initial size of shrimp used in our experiments ($p = 0.6414$). A negative relationship between initial size and growth of white shrimp was statistically significant, but explained <4% of the variation in the data ($p = 0.0046$, $R^2 = 0.0381$).

Recovery rates of experimental animals did not vary among treatments, but there was a significant location effect on recovery in the May experiment (Fig. 4). Significantly fewer brown shrimp were recovered from the Intermediate location than from the other locations in May (ANOVA: MS = 12.389, F = 13.313; $p = 0.0001$, Games–Howell critical difference = 0.139, 0.140, and 0.135). No difference was detected in the number of white shrimp recovered among locations in the September experiment (ANOVA: MS = 0.806, F = 1.018, $p = 0.39$, Fig. 4). Recovery was not related to shrimp size. The mean initial sizes and initial size frequency distributions of recovered shrimp were similar to those measured for the entire population of experimental shrimp in both experiments.

Shrimp growth rates varied among locations (Table 3, Figs. 5 and 6). Mean daily growth rates of brown shrimp within individual mesocosms in the May experiment ranged from 0.1 to 1.1 mm (17–76 mg) at the Intermediate location, 0.7–1.3 mm (44–116 mg) at the Brackish location, 0.7–1.9 mm (37–168 mg) at the Saline UE location, and 0.7–1.9 mm (47–162 mg) at the Saline DE location. For white shrimp in the September experiment, the ranges in daily growth rates among mesocosms for Intermediate, Brackish, Saline

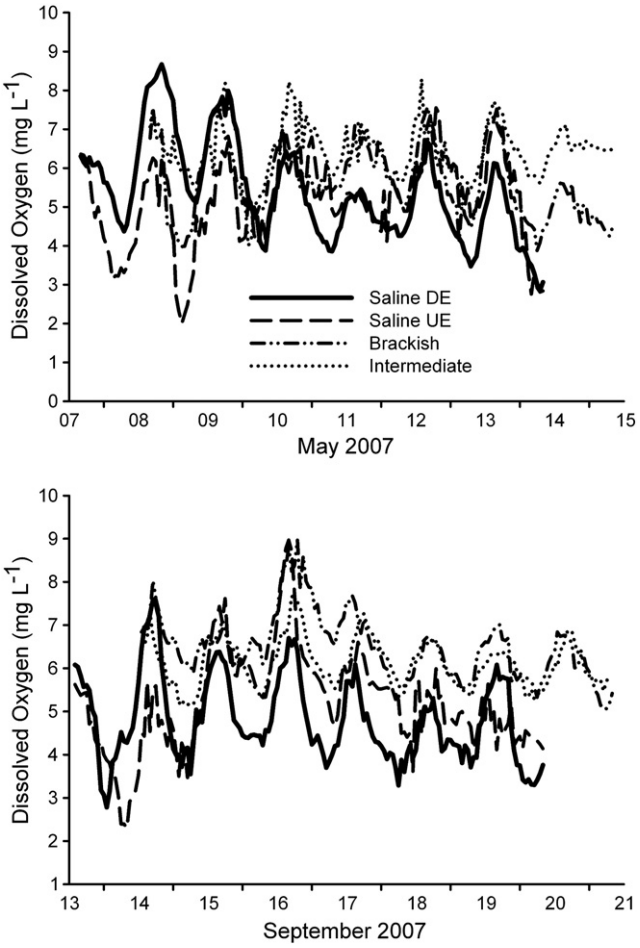

Fig. 3. Plot of dissolved oxygen concentration (mg L^{-1}) measured hourly during the May and September 2007 experiments at each location: Intermediate, Brackish, Saline UE = Saline Up Estuary, and Saline DE = Saline Down Estuary. Values in May are from one recorder each at the Intermediate, Brackish, and Saline UE locations and means from four recorders at the Saline DE location. Values in September are from one recorder each at the Brackish and Saline DE location and means from two and four recorders at the Saline UE location and Intermediate location, respectively.

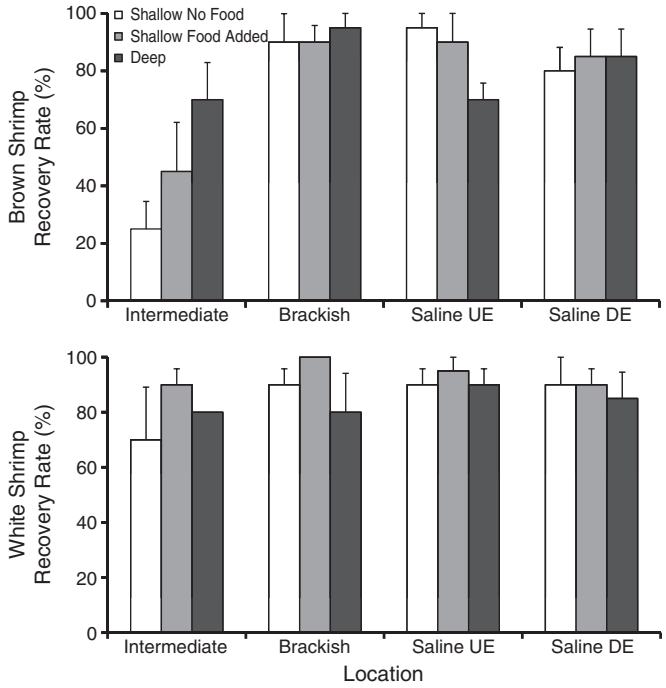

Fig. 4. Comparison of recovery rates (%) for experimental shrimp among the four locations (Intermediate, Brackish, Saline UE = Saline Up Estuary, Saline DE = Saline Down Estuary) and three treatments (shallow no food, shallow food added and deep) in the May and September 2007 experiments. Each mean and SE was calculated from four samples.

UE, and Saline DE locations were −0.1–0.9 mm (1–61 mg), 0.2–1.3 mm (16–95 mg), 0.7–1.4 mm (35–71 mg), and 0.7–1.5 mm (45–107 mg), respectively. Both brown shrimp and white shrimp grew significantly more slowly at the Intermediate location than at the other three locations (Table 3). We also computed mean (±SE) growth rates among locations as change in carapace length (CL d^{-1}) and percent body weight (%d^{-1}) to allow for comparisons using these additional response variables. Growth rates of brown shrimp were 0.12 ± 0.025, 0.23 ± 0.018, 0.25 ± 0.026, and 0.27 ± 0.026 mm CL d^{-1} at the Intermediate, Brackish, Saline UE, and Saline DE locations, respectively. White shrimp grew 0.09 ± 0.023, 0.15 ± 0.023, 0.20 ± 0.012, and 0.22 ± 0.021 mm in CL d^{-1} at the Intermediate, Brackish, Saline UE, and Saline DE locations, respectively. Growth rates as daily percent change in biomass were: brown shrimp: Intermediate = 4.5 ± 0.8, Brackish = 8.9 ± 0.6, Saline UE = 10.3 ± 1.2, Saline DE = 10.1 ± 0.9% d^{-1}; white shrimp: Intermediate = 2.7 ± 0.6, Brackish = 7.4 ± 1.1, Saline UE = 7.0 ± 0.5, Saline DE = 8.4 ± 0.7% d^{-1}.

Growth rates also differed significantly among treatments for both brown shrimp and white shrimp (Table 3, Figs. 5 and 6). Both species consistently grew more rapidly in mesocosms where food was added. Treatment interacted significantly with location for white shrimp (Table 3), as the addition of food had a much greater effect on white shrimp growth at the low salinity locations (Intermediate and Brackish) than higher salinity locations (Figs. 5 and 6). A significant treatment effect of water depth was detected for brown shrimp, but only when change in biomass was the response variable in the analysis (Table 3, Fig. 6). Brown shrimp put on more biomass at shallow than deep sites.

Potential predators recovered when the mesocosms were emptied included hardhead catfish *Ariopsis felis*, sand seatrout *Cynoscion arenarius*, spotted seatrout *Cynoscion nebulosus*, spot *Leiostomus xanthurus*, Atlantic croaker *Micropogonias undulatus*, speckled worm eel *Myrophis punctatus*, silver perch *Bairdiella chrysoura,* gulf killifish *Fundulus grandis*, gulf toadfish *Opsanus beta*, and blue crab *Callinectes sapidus*. Unmarked penaeid shrimps (potential competitors) also were collected when we cleared the mesocosms. Although we

Table 2
Summary statistics for animals used in the growth experiments conducted at four locations and on four dates using juvenile brown shrimp and white shrimp. The size range, mean size and 1 standard error (S.E.), and the total number of animals (n) used in each experiment are shown. The size classes used for each experiment to separate animals before distributing them among mesocosms also are given.

Species	Dates	Locations	Size range (mm)	Mean (mm)	S.E.	n	Size classes
Brown shrimp	May 7–14, 2007	Saline UE, Saline DE	33–64	48.3	0.71	120	≤40, 41–45, 46–50, 51–55, ≥56
	May 8–15, 2007	Intermediate, Brackish	32–61	47.7	0.71	120	≤40, 41–45, 46–50, 51–55, ≥56
White shrimp	September 13–20, 2007	Saline UE, Saline DE	34–71	48.2	0.76	120	≤40, 41–45, 46–50, 51–55, ≥56
	September 14–21, 2007	Intermediate, Brackish	34–72	48.8	0.80	120	≤40, 41–45, 46–50, 51–55, ≥56

Table 3
Comparison of mean daily growth rates of shrimp as mm d^{-1} total length and mg d^{-1} wet weight biomass and (one standard error, 1 S.E.) among four locations (Intermediate = INT, Brackish = BRACK, Saline UE = SALU and SalineDE = SALD) and three treatments (Deep = D, Shallow No Food = SNF and Shallow Food Added = SF). These data were derived from field experiments conducted on four dates in May and September 2007. Each mean was estimated from 12 to 16 samples among location and treatment, respectively (except for brown shrimp: INT = 10, SF = 15, SNF = 15). and each sample was determined by calculating the mean growth rate of experimental shrimp recovered from a field enclosure. ANOVA results (p values) are given for the main effects of location and treatment and *a priori* contrasts that compare D vs. SF and SF vs. SNF. The significant results of the Games–Howell post-hoc tests comparing growth rates among the four locations also are given.

	Location main effect								Games–Howell post-hoc comparison results	Treatment main effect						Contrast p Values		Interaction location × treatment
	Intermediate		Brackish		Saline UE		Saline DE		ANOVA *p* Value		Deep		SNF		SF		ANOVA *p* Value	D vs. SNF	SNF vs. SF	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.			Mean	S.E.	Mean	S.E.	Mean	S.E.				
Growth (mm d^{-1})																				
May 2007																				
Brown shrimp	0.6	(0.108)	1.0	(0.058)	1.2	(0.111)	1.2	(0.108)	0.0001	SALD = SALU = BRACK > INT	0.8	(0.078)	1.0	(0.078)	1.3	(0.100)	0.0004	0.2499	0.0048	0.4992
September 2007																				
White shrimp	0.4	(0.090)	0.8	(0.103)	1.0	(0.056)	1.1	(0.084)	0.0001	SALD = SALU = BRACK > INT	0.8	(0.078)	0.7	(0.120)	1.0	(0.071)	0.0001	0.1891	0.0001	0.0025
Growth (mg d^{-1})																				
May 2007																				
Brown shrimp	36.7	(6.358)	78.3	(5.392)	101.9	(11.774)	89.47	(10.639)	0.0001	SALD = SALU = BRACK > INT	56.1	(5.989)	79.9	(10.385)	100.3	(9.707)	0.0004	0.0285	0.0471	0.3495
September 2007																				
White shrimp	26.6	(5.571)	60.9	(8.153)	55.02	(3.038)	70.85	(6.052)	0.0001	SALD = SALU = BRACK > INT	50.1	(5.223)	41.0	(7.350)	68.9	(4.970)	0.0001	0.0743	0.0001	0.0014

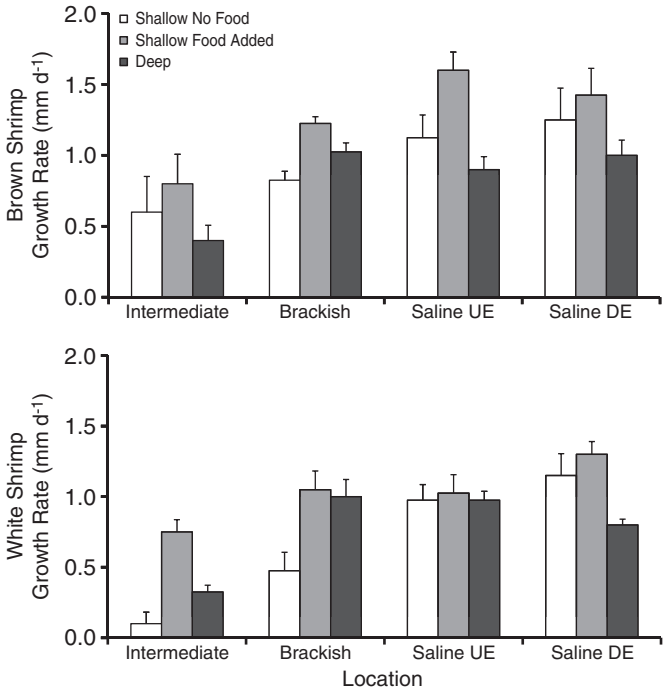

Fig. 5. Comparison of daily shrimp growth rates in length (mm d^{-1}) from the May and September 2007 experiments. Each mean and SE was calculated from four samples, except in the Intermediate location during the May experiment, only 3 samples each for the shallow no food and shallow food added treatments.

attempted to remove any animals near the outer walls of mesocosms before the drop sampler was used to recover the experimental animals, there was *ca* 5 cm of space between the drop sampler wall and the mesocosm, after the drop sampler had been lowered over the mesocosm. Any animals located within this space would have been

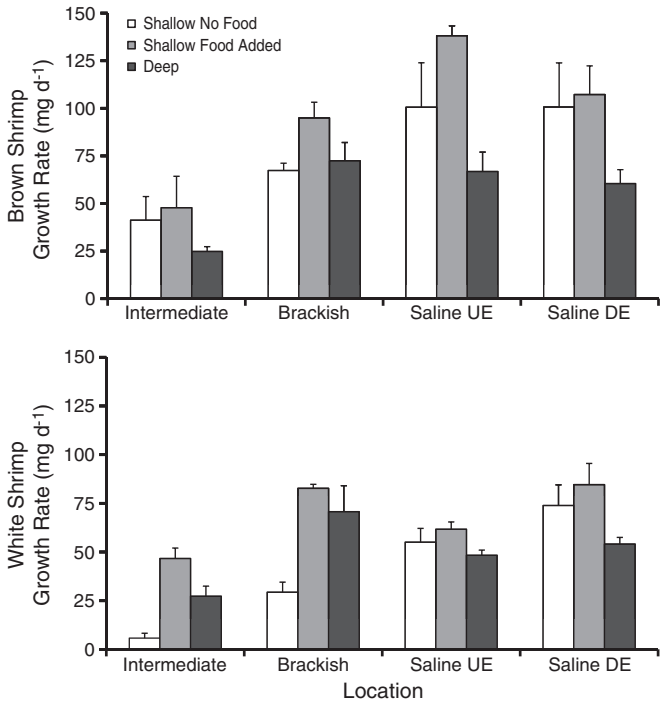

Fig. 6. Comparison of daily shrimp growth rates in biomass (mg wet weight d^{-1}) from the May and September 2007 experiments. Each mean and SE was calculated from four samples, except in the Intermediate location during the May experiment, only 3 samples each for the shallow no food and shallow food added treatments.

Table 4
Mean biomass as mg dry weight 58.9 cm^{-2} and (one standard error, 1 S.E.) of benthic infauna among four locations (Intermediate = INT, Brackish = BRACK, Saline UE = SALU and Saline DE = SALD) and three treatments (Deep = D, Shallow No Food = SNF and Shallow Food Added = SF). Each mean was estimated from 12 to 16 pooled sediment core samples collected prior to initiating shrimp growth experiments in each location and treatment, respectively. ANOVA results (p values) are given for the main effects of location and treatment and *a priori* contrasts that compare D vs. SNF and SF vs. SNF treatments. The significant results of the Games–Howell post-hoc tests comparing biomass among the four locations also are given.

	Location main effect								Games–Howell post-hoc comparison results	Treatment main effect						Contrast p Values		Interaction location × treatment
	Intermediate		Brackish		Saline UE		Saline DE		ANOVA *p* Value		Deep		SNF		SF		ANOVA *p* Value	D vs. SNF	SNF vs. SF	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.			Mean	S.E.	Mean	S.E.	Mean	S.E.				
May 2007																				
Annelids	5.7	(2.322)	6.0	(2.819)	24.5	(5.548)	46.0	(9.971)	0.0001	SALD = SALU > INT = BRACK	16.5	(4.238)	22.9	(7.888)	22.2	(7.194)	0.6549			0.4858
Crustaceans	4.1	(2.394)	4.2	(3.493)	51.6	(21.094)	22.3	(5.861)	0.0022	SALD > INT	6.5	(2.628)	22.8	(7.288)	32.4	(16.304)	0.0846			0.0079
September 2007																				
Annelids	3.5	(1.371)	4.4	(1.077)	5.5	(1.570)	7.5	(3.301)	0.4835		2.0	(0.554)	7.8	(1.373)	5.9	(2.467)	0.0440	0.0145	0.4065	0.2552
Crustaceans	11.2	(7.017)	4.5	(2.420)	14.6	(4.801)	3.3	(1.121)	0.1509		1.1	(0.536)	18.6	(5.785)	5.5	(1.787)	0.0024	0.0008	0.0100	0.5046

collected with the experimental animals. Therefore, some of the animals collected may not have been present inside the mesocosms during the experiments.

Potential infaunal prey biomass (derived from benthic sediment cores) varied among locations in the May experiment and among treatments in the September experiment (Table 4, Fig. 7). In May, the two saline locations contained more annelid biomass than the two low salinity locations (Intermediate, Brackish), and the Saline DE location had significantly more crustacean biomass than the Intermediate location. Adding food increased growth rates at the Intermediate location (by 33% in TL and 16% in Wt) and the Brackish location (48% TL and 41% Wt) where benthic prey biomass was low. Growth also was increased at the Saline UE location (42% TL and 37% Wt) and to a lesser degree at the Saline DE location (14% TL and 7% Wt), where benthic prey biomass was relatively high. By September, prey biomass at both Saline (UE and DE) locations had declined from the relatively high levels observed in May, and no location effect of prey biomass was detected in the analysis for September. Prey biomass in September, however, was higher in mesocosms located along the shore in shallow water than in mesocosms placed away from the marsh in deeper water. In addition, crustacean biomass was less in mesocosms randomly selected to receive additional food than in those identified for no additional food. Crustacean biomass in one sample, in particular, taken from the Intermediate location appeared relatively high, but dropping this outlier from the analysis did not change the results. Therefore, this difference in initial prey biomass seems to have occurred by chance and provided an opportunity for a conservative test of the effect on shrimp growth of providing additional food.

Few significant relationships were detected in the regression analyses between shrimp growth and the biomass of nekton we recovered at the end of each experiment. An examination of scatter plots suggested that these significant relationships were linear. There was a significant positive relationship between the biomass of total penaeids recovered from the enclosures and shrimp growth expressed as biomass increase per day in the September experiment

Fig. 7. Comparison of prey (annelids and crustaceans) biomass (mg dry weight 58.9 cm^{-2}) among the four locations (Intermediate, Brackish, Saline UE = Saline Up Estuary, Saline DE = Saline Down Estuary) and three treatments (shallow no food, shallow food added and deep) in the May and September 2007 experiments. Each mean and SE was calculated from four sediment samples.

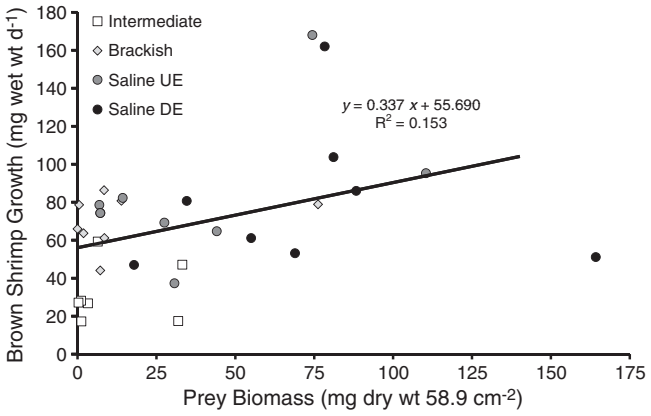

Fig. 8. Relationship between brown shrimp *Farfantepenaeus aztecus* growth rate and the biomass of potential prey (annelids and crustaceans) collected from sediment cores taken before initiating May 2007 growth experiments. Data from mesocosms where food was added are not included.

(d.f. = 1,47; p = 0.0017), and this relationship explained about 19% of the variability in the data. There also was a significant positive relationship between shrimp growth in biomass and the biomass of potential prey in the benthic core samples we collected prior to initiating the experiments. This relationship was statistically significant only for brown shrimp in the May experiment (Fig. 8).

5. Discussion

Shrimp growth was significantly higher at the high salinity locations. Brown shrimp at the Saline DE location grew 2.1 times faster (in length) and added 2.4 times more biomass each day than those at the Intermediate location. Similarly, white shrimp grew 2.8 times faster and added 2.7 times more biomass each day at the Saline DE than Intermediate location. Although our results clearly show that shrimp growth rates differed among locations, it is difficult to identify with certainty the factors responsible for these differences.

Our study only examined 1–2 locations in each salinity zone, and therefore, it was not possible to examine variability among locations within zones. This problem with pseudoreplication (Hurlbert, 1984) was unavoidable due to the constraints required in setting up and running these experiments. Our design would have provided greater inferential power had we randomly located mesocosm sites within salinity zones across the entire estuary, or better yet, across several different estuaries. Attending to 48 mesocosms scattered across large areas within each zone, however, would have been unmanageable.

Salinity, as expected, was much lower at the Intermediate location (<2) than the other locations during the experiments, and the growth of shrimp confined to this low salinity location may have been negatively affected by the metabolic cost of osmoregulation. The ability of penaeid shrimps to osmoregulate varies with species, developmental stage, and temperature (Williams, 1960; Dall et al., 1990; Lemaire et al., 2002). Although both species show a wide capacity for osmoregulation, white shrimp appear to have better regulatory capabilities in low salinity waters than brown shrimp (McFarland and Lee, 1963; Castille and Lawrence, 1981). Shrimp use osmoregulation to maintain a constant hemolymph concentration in low salinity. The physiological mechanisms used for this osmoregulation include an increase in permeability to water, active uptake of ions, and liberation of amino acids to the hemolymph (Rosas et al., 1999). Amino acids are more important than ions for maintaining osmotic pressure in white shrimp and brown shrimp, and the pool of amino acids involved in osmoregulation is deaminated and subsequently excreted as ammonia (McFarland and Lee, 1963; Rosas et al., 1999). The regulatory capacity of ammonia excretion depends on proteins from digested food (Rosas et al., 1999), and any food used for this purpose cannot go toward increasing somatic growth. Therefore, juvenile shrimp in low salinity environments may grow more slowly because energy that would otherwise be allocated to somatic growth must be used for osmoregulation.

The results of laboratory studies, where variables other than salinity are carefully controlled, show that the growth of penaeid shrimps and other animals are reduced in low salinity. Young brown shrimp grow more slowly in salinities of 2 and 4 than 8 and 12 (Saoud and Davis, 2003). Pink shrimp *Farfantepenaeus duorarum* grow most rapidly at a salinity of 30, and growth rates decline as salinity either decreases or increases from this value (Browder et al., 2002). Brown shrimp and white shrimp cultured in ponds of three different salinities (7, 15, 21) grow more slowly and experience higher mortality at the lowest salinity (Hysmith and Colura, 1976). Although juvenile blue crabs can survive>2 months in freshwater (Guerin and Stickle, 1992), they grow more slowly in low salinity. Blue crab growth rates are lower at a salinity of 3 than salinities of 15 and 30 (Cadman and Weinstein, 1988). The optimal salinity for growth in juvenile weakfish *Cynoscion regalis* and juvenile mullet *Mugil* sp. is 20 and 17, respectively, and growth in these species is reduced at lower salinities (Lankford and Targett, 1994; Peterson et al., 2000).

Although the energy requirements of osmoregulation may affect growth at very low salinities, Dall et al. (1990) concluded that acclimated penaeid shrimps generally require little energy for osmoregulation unless salinity is changing rapidly. Salinity also could affect shrimp growth rates indirectly, however, by influencing the abundance and distribution of their food. Penaeid shrimp feed on a variety of shallow-burrowing benthic infauna, especially annelids and small crustaceans (McTigue and Zimmerman, 1998; Fry et al., 2003; Beseres and Feller, 2007). In May of our study, potential prey biomass (small crustaceans and annelids in benthic cores) was lowest at the low salinity locations (Intermediate and Brackish). There was a positive relationship between brown shrimp growth and the biomass of these prey organisms, and adding additional food increased shrimp growth at the low salinity locations. The addition of food also increased growth at the saline locations, but this increase was lowest at the Saline DE location. These results suggest that salinity/location effects on brown shrimp growth were related to prey abundance. In contrast to our results, Posey et al. (2005) suggest that a greater prey base for blue crabs in oligohaline areas compensates for the increased metabolic demands associated with low salinity conditions there.

White shrimp held at the Intermediate location grew more slowly than those at the other locations, but their growth rates were not related to the biomass of infaunal crustaceans and annelids. The biomass of these benthic prey was relatively low at all locations in September (<1/3 that measured in May), with no significant difference among locations. Benthic infaunal populations vary seasonally and generally reach a low point in summer or fall when we conducted the experiment with white shrimp (Service and Feller, 1991; Whaley and Minello, 2002). Despite the low biomass of these potential benthic prey in September, white shrimp growth rates in the mesocosms were similar to those of brown shrimp in May, suggesting that white shrimp rely on other food sources in addition to benthic infauna (McTigue and Zimmerman, 1991, 1998). The addition of food in mesocosms greatly increased white shrimp growth rates at the two low salinity locations, especially at the Intermediate location where grow rates increased>six times when we added food. In contrast, the addition of food at the two high salinity locations increased white shrimp growth rates very little (i.e., no more than 15%).

The positive response to the addition of food by both brown shrimp and white shrimp everywhere, including the high salinity location, where the energy demand for osmoregulation is expected to be low, may indicate that growth was food limited at all locations. Although shrimp growth rates in our study were positively, not negatively, related to the total biomass of shrimp (including unmarked shrimp) in mesocosms, high shrimp densities can affect growth. Density had a

significant effect on the growth of white shrimp in field experiments conducted in North Carolina where growth rates decreased as shrimp densities were increased from 5 to 20 m^{-2} (Yip-Hoi, 2003). Low shrimp growth rates also have been attributed to high densities in Celestun lagoon, Mexico (Pérez-Casteñeda and Defeo, 2005). Although we used a stocking density of only 5 shrimp $mesocosm^{-1}$, additional unmarked shrimp (mean number ± SE $mesocosm^{-1}$: brown shrimp: Intermediate = 1.2 ± 0.30, Brackish = 1.0 ± 0.25, Saline UE = 2.3 ± 0.45, Saline DE = 4.2 ± 0.30; white shrimp: Intermediate = 3.3 ± 0.73, Brackish = 1.7 ± 0.41, Saline UE = 3.0 ± 0.41, Saline DE = 1.3 ± 0.35) were recovered at the end of each experiment. These additional shrimp increased our stocking density by an average of 20–84% if they were enclosed when the mesocosms were set in place before initiating each experiment. Assuming these additional shrimp increased the original stocking density, the densities inside our enclosures exceeded those that occur naturally in marsh ponds of Barataria Bay at high tide (Rozas and Minello, 2010), but may have been similar to low-tide densities in ponds and were lower than those (10 or 20 m^{-2}) shown by Yip-Hoi (2003) to elicit a negative effect on growth. As growth rates for the shrimp in our experiments were similar to those estimated for free ranging shrimp (St. Amant et al., 1966), our results suggest that shrimp growth may be food limited throughout the estuary.

In neither experiment did the addition of food fully compensate for the negative effect on the growth of animals confined to the Intermediate location. Even with additional food, mean growth rates of shrimp at the Intermediate location were less than those of shrimp at the high salinity location that received no additional food (brown shrimp: 0.8 vs. 1.3 mm d^{-1}; 48 vs. 101 mg d^{-1}; white shrimp: 0.8 vs. 1.2 mm d^{-1}; 47 vs. 74 mg d^{-1}).

Although our attempt to incorporate temperature as a treatment in our experiments was unsuccessful, previous studies show that temperature often has a greater affect on the growth of estuarine organisms than salinity (Cadman and Weinstein, 1988; Vernberg and Piyatiratitivorakul, 1998; Rakocinski et al., 2002). Moreover, temperature can interact with salinity to affect osmoregulation and growth rates in estuarine animals (Williams, 1960; Zein-Eldin and Aldrich, 1965; Bishop et al., 1980; Lankford and Targett, 1994). There is a real need for carefully controlled laboratory experiments to examine how the combination of temperature and salinity affect the growth rates of juvenile brown shrimp and juvenile white shrimp. The design of these experiments should include the wide range of temperature and salinity encountered by penaeid shrimp in estuarine nursery areas. These experiments would provide a better understanding of the relationship between the estuarine environment and the abundance, distribution, and production of coastal shrimp populations (Browder et al., 2002; Diop et al., 2007).

Possible artifacts of any experiment are always a concern. The mesocosms used in this study allowed us to measure growth rates of shrimp confined to specific locations along an estuarine salinity gradient. The differences in growth rates documented in our study should represent location and treatment differences if mesocosm effects were minimal or if any such effects were similar among locations and treatments (Peterson and Black, 1994; Underwood, 1997; Stunz et al., 2002). Several steps were taken to minimize experimental artifacts. We used a stocking density similar to natural densities in the estuary. The spatial layout of treatments was randomized and each treatment was replicated. We limited the duration of our experiments to 7 days to reduce the possibility of depleting benthic prey or causing excessive fouling of mesocosm walls and sedimentation inside the mesocosms. The netting that composed the mesocosm walls allowed free water exchange and enabled environmental conditions inside and outside the enclosures to equilibrate. The porous walls also allowed entry of planktonic prey. We measured environmental variables that might affect growth both within and outside the mesocosms to determine whether experimental artifacts may have affected our results. We minimized the time between the capture of experimental shrimp and their transfer into the mesocosms to limit stress on these animals. The growth rates of shrimp in our experiments were similar to those measured under natural conditions (St. Amant et al., 1966; Knudsen et al., 1977), and we interpreted this similarity as an indication that mesocosm artifacts were minimal. High survival rates in most experimental mesocosms also indicate that artifacts were negligible. Recovery rates were relatively high except for the mesocosms in shallow water at the Intermediate location in the May experiment. The low recovery rates at these sites were likely due, at least in part, to the escape of brown shrimp near the end of the experiment when storm-generated waves partially lifted the bottom of some mesocosms from the substrate. We recovered no shrimp from two of the mesocosms, and recovery rates from several other mesocosms were very low.

Previous studies have measured growth rates of juvenile brown shrimp and white shrimp, but none of these included low salinity environments. In our study, which included Intermediate to saline environments, mean daily growth rates of brown shrimp in mesocosms where no additional food was provided were 0.4–1.3 mm d^{-1}, and these rates are comparable to those reported from earlier studies. In an experiment conducted in Galveston Bay, brown shrimp held for 27 day in cages without marsh vegetation grew on average 0.8–1.0 mm d^{-1} (Minello and Zimmerman, 1991). Knudsen et al. (1977) estimated growth rates of 0.5–0.9 mm d^{-1} for free ranging brown shrimp in a Louisiana marsh, whereas Wheeler (1969) reported a rate of 1.0 mm d^{-1} for brown shrimp grown in fertilized ponds. Hysmith and Colura (1976) increased growth rates of pond-reared brown shrimp to 2 mm d^{-1} with supplemental feed. St. Amant et al. (1966) related changes in growth rates for free ranging brown shrimp in Louisiana to changes in water temperature and reported average growth rates of <1.0 mm d^{-1} at <20 °C and <1.5 mm d^{-1} at <25 °C. A mean growth rate of 1.4 mm d^{-1} was documented for brown shrimp held in acrylic enclosures within a small marsh pond in Louisiana (Fry et al., 2003). Brown shrimp fed *ad libitum* in laboratory experiments grew up to 0.95 mm d^{-1} (Venkataramiah et al., 1975). Slower rates (0.2–0.3 mm d^{-1}) documented for brown shrimp grown in the laboratory on benthic cores extracted from marsh sediment were attributed to food limitation (Whaley, 1997; Minello et al., 2003). The mean daily growth rates of 0.1–1.2 mm d^{-1} for white shrimp in our experiments span the range of those measured in some earlier studies. White shrimp enclosed for 27 days in cages without vegetation in Galveston Bay grew an average of 1.1 mm d^{-1} (Minello and Zimmerman, 1991). In a more recent study, white shrimp caged in a shallow non-vegetated pond near Galveston Bay grew an average of 0.8 mm d^{-1} in summer and 0.9 mm d^{-1} in fall (Baker and Minello, 2010). More rapid growth rates of 2.1–2.5 mm d^{-1} were reported for white shrimp grown in aquaculture ponds (Johnson and Fielding, 1956; Wheeler, 1969; Hysmith and Colura, 1976), and relatively slow growth rates for shrimp reared in the laboratory (0.2–0.4 mm d^{-1}, Kneib and Huggler, 2001) or over shallow non-vegetated bottom (0.3 mm d^{-1}) at Grand Bay National Estuarine Research Reserve, Mississippi (Shervette and Gelwick, 2008).

Our experiments clearly demonstrate that growth rates of brown shrimp and white shrimp are significantly reduced in low-salinity habitat. Densities of these species also are relatively low in this habitat compared to those in the Saline zone of the lower estuary (Zimmerman et al., 1990; Peterson and Ross, 1991; Howe et al., 1999; Rozas and Minello, 2010). Freshwater diversions that reduce estuarine salinity over a large portion of available habitat during the peak recruitment periods for these species could reduce the productivity of brown shrimp and white shrimp within the estuary. The impact on shrimp productivity would depend on the magnitude, duration, and timing of freshwater input. Potential impacts, however, could be ameliorated by avoiding large releases during peak recruitment periods, using high flows in El Niño years when shrimp populations are expected to be relatively low anyway, and operating diversion structures in other ways that minimize

the potential negative effects of freshwater releases on fishery populations (Day et al., 2009; Adamack et al., in review; Piazza et al., 2010).

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